Soft Corals: Chemistry and Ecology

by John C. Coll, and Paul W. Sammarco

Soft corals (Coelenterata: Alcyonacea) are one of the most important groups of animals on the Great Barrier Reef. They are abundant over the 2,000 kilometers of this reef complex and are a most diverse group, possessing hundreds of different species. They occur as attached colonial organisms, with each colony made up of thousands of interconnected individual and identical polyps. They vary widely in form from the soft and fleshy members of the Xeniidae family to the very beautiful but prickly members of the genus *Dendronephthya*, and from the hard, leatherlike forms of the genus *Sinularia* (*S. dura*) to other erect, tree-like forms of the same genus (*S. flexibilis*) (Figures 1–4).

Soft corals produce natural compounds that play important roles in their ecology—particularly in their defense against predators, in competition for space, and in reproduction. These secondary compounds are novel in structure. The majority of them belong to the chemical class called terpenes*, and are responsible for the odors and distastefulness of common plants and trees such as pines, eucalyptus, sagebrush, and so on. These compounds (and hence the organisms which produce them) interest natural-products chemists because of their potential application as pharmaceutical agents (for example, antibiotics, antifungal agents, and antitumoral agents).

These compounds appear to offer a distinct adaptive advantage to the organisms that possess them, helping them to survive in their natural environment. In any community, particularly where organisms are sessile (permanently attached to the bottom), interactions between individuals can become intense (Figure 5).

Toxicity As Protection Against Predation

In general, coral reefs possess many would-be predators—fish, crustaceans, echinoderms, and so on. Most common soft corals are fleshy in texture and thus appear defenseless against predators. Chemical analysis suggests that they are rich in nutritionally important substances (such as protein, fats, and carbohydrates) and could serve as a valuable food source to predators. Yet, recent surveys show that the incidence of predation on this group is low.

In contrast, hard corals constitute a major food source for some common groups of reef fish: parrotfish, starfish (crown-of-thorns), mollusks, and crabs. Soft corals thus appear to possess defenses not immediately obvious to the observer. Chemical analyses have revealed high concentrations of certain terpenoid compounds in many soft corals that may serve as a defense mechanism.

Laboratory tests have been performed on the mosquito-fish (*Gambusia affinis*) using aqueous extracts of numerous soft corals collected over the full range of the Great Barrier Reef. These tests show that about 50 percent of the extracts are toxic. In addition, the level of toxicity across families and between species varies greatly, ranging from lethal to harmless. Because toxicity does not seem to account entirely for the very low levels of predation observed in the field, other defenses are suspected.

Feeding Deterrence

Tests also were performed to determine whether soft coral extracts possessed characteristics which rendered them distasteful to fish. We impregnated standard tropical fish food with soft coral extracts of various concentrations and then tested them for feeding deterrence in test fish. Almost 90 percent of the samples possessing the highest amounts of extract were found to deter from feeding. Even at the lowest concentration, 55 percent of the samples still elicited the same response—suggesting that feeding deterrence is a common characteristic of soft corals.

However, no easily definable link or positive relationship was found between the incidence of toxicity and that of feeding deterrence. Some very unpalatable soft corals were shown to be harmless while apparently palatable soft corals were lethal. Thus, these characteristics, toxicity and feeding deterrence, 1) probably evolved independently, 2) may involve different sets of chemical compounds, or 3) may represent adaptations that simply perform different rather than dual functions in the organism.

* Any of certain types of organic compounds present in essential oils of plants.

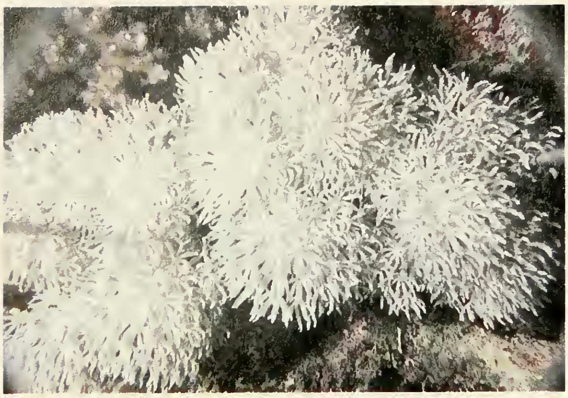

Figure 1. The Xenia *species is soft, like firm gelatin, with non-retractile, fully exposed polyps. (All photos courtesy of John Coll unless otherwise indicated.)*

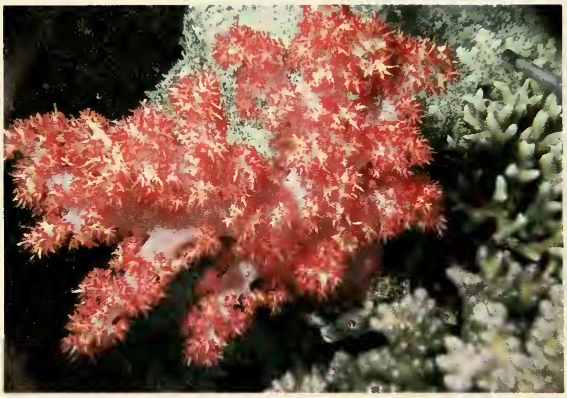

Figure 2. The colorful Dendronephthya *species' polyps are protected by small spicules composed of needle-like pieces of calcium carbonate.*

Predation

As mentioned previously, soft corals vary in structure and form (morphology), particularly regarding characteristics that protect either the polyps or the colony as a whole from predation. Another type of protection—toxicity—varies widely in both its occurrence within species and its intensity. A positive relationship has now been found between the lack of physical defense characteristics and toxicity to fish. Soft corals that bear physical defenses against predators seem to be less likely to be toxic to fish.

Soft corals, such as *Sarcophyton* can retract their polyps completely inside the surface layer of the colony (Figure 6), while the polyps of others, such as *Xenia* and *Cespitularia*, are constantly exposed (Figure 7). Another type of polyp and colony defense involves small sharp calcium carbonate spicules. These long, needle-like parts often surround and protect the polyp-head in a canopy-like fashion (Figure 8). In other colonies, such as *Sinularia dura*, the spicules are tightly packed throughout the body of the colony, and the polyps can retract completely into a protected area. Other species exhibit a combination of these characteristics: *Sinularia flexibilis* possesses a heavily spiculated base, devoid of polyps, but with soft flexible branches into which polyps can completely withdraw.

Neither these physical mechanisms nor toxicity guarantees safety against predators. Some specialized predators feed on highly toxic species of soft corals. Examples of this type of coevolution may also be found in the terrestrial environment. A *Chrysalina* sp. beetle—immune to the effects of the secondary compound hypericin—feeds largely on the toxic fruit and leaves of *Hypericum* sp. This opens up a food source to the species generally unavailable to other predators. Mollusks are the major group in the marine environment from which several such predators have evolved. On the Great Barrier Reef, the egg cowrie *Ovula ovum* feeds almost exclusively on soft corals of the genus *Sarcophyton* (Figure 9). This gastropod is capable of transforming the highly toxic sarcophytoxide into a less toxic compound without ill effects. A similar example of predators modifying the toxins of their prey may be found in other nudibranchs,* such as *Aplysia californica*, which prey on algae.

Some predators even exploit the toxins of their prey. Immune to the toxic molecules, they store them in specialized glands in the outer surface of their body. The aeolid nudibranch *Phyllodesmium longicirra* selectively stores toxins from *Sarcophyton trocheliophorum* in its cerata** but not in other parts of its body. If predatory fish attack, the cerata may be autotomized (voluntarily detached). In this way, the predator is provided with an unpalatable if not toxic sample of food. Similar examples may be found in other nudibranchs, particularly *Phyllidia*.

Competition for Space

The use of chemicals is not limited to fending off predators. They also are employed in competing for living space with other species as well as with other soft corals. Many sessile, colonial organisms on coral reefs possess specialized mechanisms that allow them to maintain and expand their living space, a resource that can be limiting in a crowded community. Hard corals possess elaborate mechanisms, such as nematocysts or stinging cells on their tentacles, to kill neighboring sessile organisms; these long, specialized sweeper tentacles can extend up to 15 centimeters—many times the length of the polyp. Mesenterial filaments, digestive filaments that extrude from the gut, are capable of extracoelenteric digestion. Soft corals, on the other hand, possess none of these apparatus and depend on other adaptations, such as their chemical composition, to maintain living space.

We hypothesized that the toxins present in soft corals may help them compete for space, a hypothesis supported by observations of retarded growth and dead tissue in hard corals adjacent to

* Any mollusks of the order Nudibranchia.

** Long tubular projections on the backs of aeolid nudibranchs.

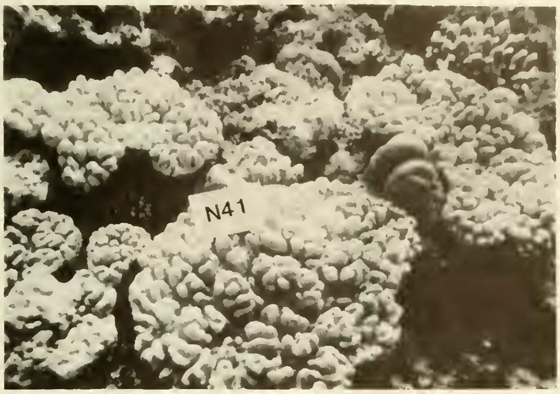

Figure 3. Sinularia *is an encrusting soft coral with hard tissue. Common on the reef crest where wave action is intense, this soft coral exhibits low relief profile.*

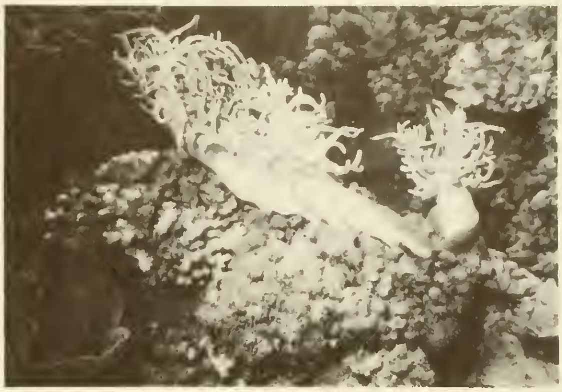

Figure 4. Sinularia flexibilis *is one of the most common soft corals found throughout the Indo-Pacific region especially in areas with high currents.*

toxic soft corals (Figure 10). Selecting several common species of both soft and hard corals, we performed manipulative relocation experiments, demonstrating that this effect was indeed significant and reproducible in the field. It first appeared that soft corals were immune to the harmful effects of hard corals, such as *Porites andrewsi* and *Pavona cactus*. A subsequent experiment, however, showed that some soft corals do in fact suffer local mortality from hard corals. Our most striking find was the incidence of local mortality, tissue necrosis,* and growth retardation in hard corals occurring without contact. This is an example of allelopathy in the marine environment—the influence of one living organism on another due to secretion of toxic substances.

To illustrate that the observed effect was indeed caused by chemicals transmitted through the water column from soft corals, a submersible water sampling device was developed. It was selective for organic molecules suspended or dissolved in seawater. Compounds found in the water surrounding one of the most toxic and most effective allelopathic soft corals were identical to those within the organism. To confirm that these toxins were indeed the active allelopathic agents, pure crystalline samples of chemicals from the soft corals were dissolved in seawater and then tested in the laboratory for potency. The pure compound killed both *Porites andrewsi* and *Acropora formosa* at concentrations of less than or equal to 10 parts per million.

Soft corals have other mechanisms that protect them from the harmful effects of scleractinian or hard corals. For example, some can secrete a protective polysaccharide layer in areas close to or in contact with the hard coral's tentacles (Figure 11). This layer then allows soft corals to overgrow living scleractinian tissue by providing a base for colony attachment and expansion. Once attachment is complete, movement across a living scleractinian coral can occur through directional growth. A good example of this is *Nephthea brassica* moving across the plating scleractinian coral *Acropora hyacinthus*.

Competition between soft corals also occurs

* The pathologic death of living tissue in a plant or animal.

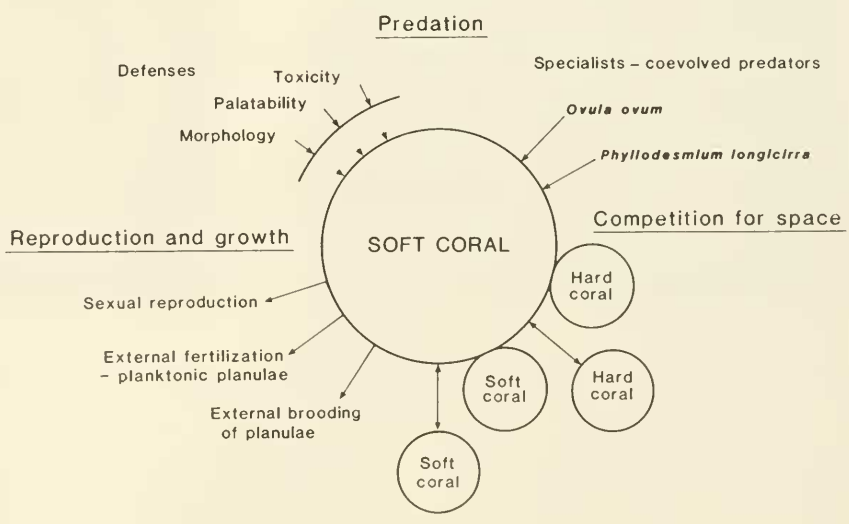

Figure 5. Summary of ecological interactions in soft corals that are chemically mediated by secondary compounds such as terpenes.

for space. The same effects of local mortality and tissue necrosis may be observed in the field, but at a much lower frequency. Manipulative experiments have confirmed that these effects are similarly chemically mediated and are experimentally reproducible in the field. Our experiments also explained the apparent low frequency of observations of these interactions in the field at any one time. Upon contact with soft corals, localized tissue necrosis occurs very rapidly, but within several days an avoidance response occurs as the two colonies bend away from each other. This is followed by a somewhat slower but longer term reaction whereby each colony moves away from the other in a manner analogous to that in *Nephthea brassica*. Soft corals can move and space themselves in their environment, which helps them to decrease the probability of contact with potential competitors.

Chemicals and Reproduction

Chemical ecology not only helps soft corals defend themselves and their living space from others, but also may play a role in reproduction. Although little is known about the reproductive biology of the Alcyonacea (soft corals), a number of interesting facts have recently emerged. Soft corals are now known to reproduce three ways: 1) externally fertilized eggs are brooded on the surface of the soft coral, 2) externally fertilized eggs develop planktonically in the water column, and 3) asexual reproduction occurs via colony growth and fragmentation. The last of these includes production of stolons* and runners.

The concentration of major secondary compounds in certain soft corals varies markedly throughout their reproductive cycles. A recent study covering the period immediately preceding and subsequent to ovulation showed that certain toxic metabolites increase markedly during the month prior to ovulation. These same compounds also were found in high concentrations in the eggs released from the same colonies (*Sinularia spp.*) and were virtually absent several months later after the peak reproductive season.

Further insights into the complexity of the terpenes' role in soft coral reproduction were derived from the chemical composition of two species of *Lobophytum*. In the case of *L. compactum*, the story parallels that of *Sinularia* above, with one compound found exclusively within the eggs of the soft coral. In the other species, *L. crassum*, the major terpene present in the soft coral was completely absent in the eggs. Thus, the chemicals may possess ecological functions that vary even between related species.

* Stem-like structures from which new individuals within a colony develop by budding.

Studies Under Way

Studies are presently under way to investigate three possible roles these chemicals may play: 1) toxicity or feeding deterrence in potential predators; 2) chemotaxis—for these chemicals may play a role in attracting sperm to the egg, and 3) accumulation of the chemicals, acting as a stimulus, indicator, or trigger for release of gametes.* At present, the chemical ecology of soft corals is not fully understood. Since 50 percent of the species possess chemicals—in particular terpenes—that may be the basis of important interactions both among themselves and within the larger ecology of the Great Barrier Reef, secondary compounds may be a major contributing factor to the evolutionary success and abundance of soft corals on the Great Barrier Reef.

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* A mature egg or sperm capable of participating in fertilization.

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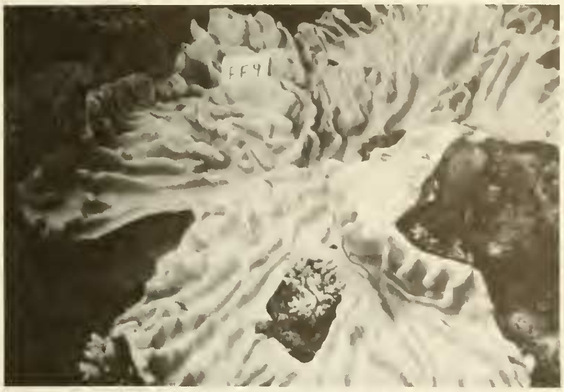

Figure 6. The Lobophytum *species is commonly found on reef crests and exhibits a colony form with low relief.*

Figure 7. A species of Cespitularia *exhibiting a soft flexible body with polyps permanently exposed to potential predators.*

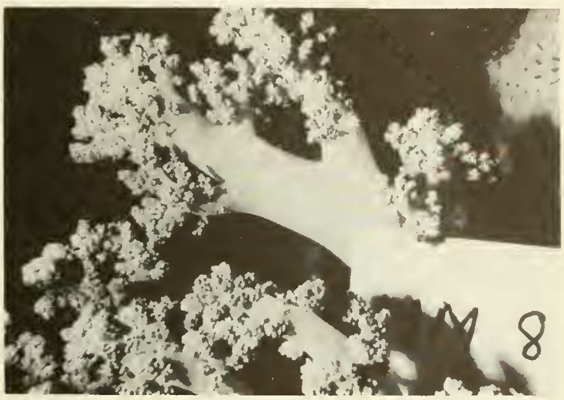

Figure 8. The tree-like Nephthea *species has polyps that are grouped at the ends of its branches; each polyp is protected by micro-spicules.*

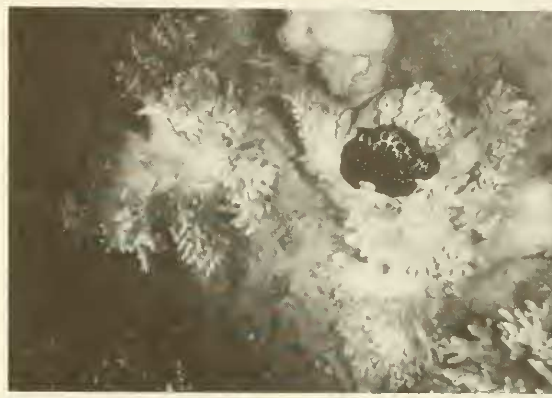

Figure 9. The egg cowrie Ovula ovum *can ingest and assimilate some highly toxic soft corals without ill effects. The shell is white, but when feeding, the mantle of the mollusk covers the shell giving it a black appearance.*

Figure 10. A large colony of Sinularia flexibilis *releasing chemicals into the surrounding water that can kill or inhibit growth in the nearby hard coral* Pavona cactus. *(Photo courtesy of Bette Willis.)*

Figure 11. A colony of Nephthea brassica *growing on live* Acropora hyacinthus. *Note the dark brown cuticle secreted by the soft coral. (Photo courtesy of Stephane LaBarre)*